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Sexual Dimorphism and Niche Divergence in a Mid-Water Octopod (Cephalopoda: Bolitaenidae)

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Abstract. In the translucent mid-water octopod *Eledonella pygmaea*, the posterior salivary glands that release proteolytic enzymes into the esophageal crop grow five times faster in males than in females. I suggest that the sexes vertically partition the water column and that large glands have evolved in males as a result of their deep-water habitat. Members of the species undergo ontogenetic vertical descent and are suggested to mate at the lower end of the adult depth range where receptive females signal males with light organs. Selection for increased fitness is inferred to result in females increasing their fecundity by feeding at the upper limit of the adult range and in mature males increasing their encounters with mates by living at depths where mating occurs. To further increase their fitness, mature males—despite occurring in a prey-limited habitat—must expend energy to visually detect potential mates, to travel over wide areas, and to attempt to copulate. To increase the energy available to them, males at depth may exploit bioluminescent prey. The large glands protect the translucent males from increased predation by physically blocking light emitted by bioluminescent prey in their crops, and by speeding digestion.

Introduction

Because it acts directly on sexually dimorphic traits, sexual selection, produced by interaction between the sexes, has been assigned a primary role in the evolution and maintenance of sexual dimorphism. Ecological factors contribute to, and theoretically drive, the evolution of sexual dimorphism but are rarely considered to be major factors in its evolution (Slatkin, 1984; Shine, 1989). Slatkin (1984) noted three ways in which ecological factors, produced by the interaction of members of each sex with the environment, could result in sexual dimorphism. Sexual dimorphism could evolve when a species has a dimorphic niche, due to sex-linked differences in ecological or social roles, when two or more optima exist for both sexes, or when very high competitive pressure results in divergence of the niches the sexes occupy, allowing resource partitioning. Selander (1972) argued that ecological factors are most likely to result in sexual dimorphism of the trophic organs, although this need not always be the case.

This paper describes sexual dimorphism in posterior salivary gland size in the mid-water octopod *Eledonella pygmaea* Verrill. Selection on males to find mates and on females to increase their fecundity is hypothesized to have led to sexually dimorphic niches. Dimorphism in the glands, which are thought to produce and release proteolytic enzymes (Boucaud-Camou and Boucher-Rodoni, 1983), is hypothesized to be due to the divergence of posterior salivary gland growth in males, as an ecological adaptation to their deep-water distribution.

Biology of Eledonella pygmaea *Verrill*

Members of the species *Eledonella pygmaea*, typical of the little-known bolitaenid octopods, occur at depths greater than 100 m in mid-latitudes (Thore, 1949). Members of the family Bolitaenidae descend in the water column as they mature. Although juveniles occur near the upper limits of the species range, larger individuals occur variably between depths of 500 and 3250 m (Thore, 1949; Young, 1978). Gravid and nearly gravid females are collected only from the deepest part of the species range, although brooding females are collected from shallow depths of the adult range. This distributional pattern led Young (1978) to conclude that mating occurs at the lower limit of the species depth range and that hatchlings are released near the upper limit of the adult distribution.

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Fully mature males, defined as those carrying spermatophores (Mangold, 1987), have not to my knowledge been reported in the literature. Low-density salts contained in fluid-filled vacuoles in the arm and mantle musculature may allow the animals to approach neutral buoyancy (Denton and Shaw, 1961). The fluid in the muscles may also increase the translucence of the animals and their susceptibility to severe damage during trawl collection, a feature which precludes direct behavioral observations of the animals.

The general anatomy of the anterior digestive system is typical of incirrate octopods (Thore, 1949), all of which are predators. The esophagus and its diverticulum, the crop, lie on the dorsal surface of the digestive gland within the mantle cavity (Fig. 1). A pair of posterior salivary glands straddle the esophagus at the level of the crop diverticulum (Fig. 1); the anterior salivary glands are attached to the buccal mass. Two ducts, one from each posterior salivary gland, merge to follow the esophagus anteriorly to the buccal mass at the center of the arms. A second duct from each gland enters the crop diverticulum directly. The opening of the crop is muscular, but its saccular portion, in preserved specimens, is nearly transparent. As in all incirrate octopods, the dorsal viscera are covered by a sheath that carries chromatophore organs. The distribution of these organs is distinctive in bolitaenids; few chromatophore organs are broadly scattered over the dorsal crop, but chromatophore organs are densely packed over the stomach, just dorsal to the tip of the mantle.

Females of *E. pygmaea* and other bolitaenids develop a circumoral light organ at sexual maturity, apparently to attract potential mates (Robison and Young, 1981). The light organ is probably not used in feeding, first because the octopod could not see prey attracted to it, and second because the green color of the emitted light is thought to be ineffective in luring prey (Robison and Young, 1981). Females are not thought to feed after the circumoral light organ develops.

Mature females are characterized by the circumoral light organ and increased pigmentation on the web and arm crown (Rancurel, 1970, Plate II; Robison and Young, 1981). Females brooding eggs are characterized by a sealed buccal mass, a deep web, and deterioration of the digestive system (Young, 1972a; 1978). As females become senescent, their consistency becomes very gelatinous, parasites

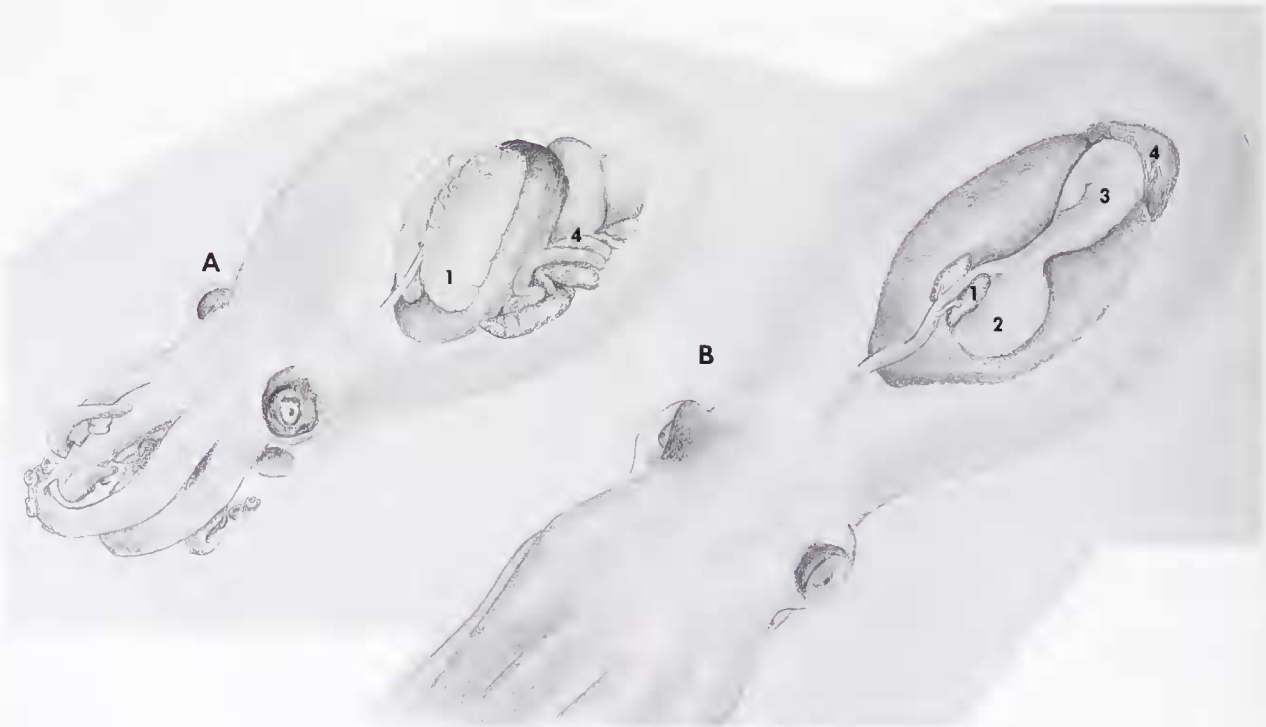

Figure 1. An oblique view of a male (A) and a dorsal view of a female (B) specimen of *Eledonella pygmaea*. The dorsal mantle has been removed in both specimens to show the esophagus entering the mantle cavity and the posterior salivary glands (1) on the dorsal surface of the digestive gland which, in the female (B), straddles the esophageal crop (2). (1) the posterior salivary glands; (2) esophageal crop, visible only in the female (B); (3) stomach, visible only in (B) after removal of the overlying membrane with its chromatophore organs; and (4) the gonad and (in A) the accessory male ducts.

become more prominent, and the digestive gland is reduced and becomes nearly transparent (Young, 1978; Voight, pers. obs.). Deterioration of the digestive organs supports the hypothesis that bolitaenids produce a single clutch of eggs, as is typical of octopods (Mangold, 1987). In addition, females probably brood their eggs in their arm crown until the eggs hatch (Young, 1972a). As the mouth is at the center of the arm crown, brooding eggs would be inconsistent with feeding.

In laboratory experiments, bioluminescence has been elicited from the digestive glands of 10 bolitaenid specimens, collected near Oahu, Hawaii, and identified as *E. pygmaea* and *Japetella diaphana* (Young *et al.*, 1979). The digestive glands of "most specimens of both species" (Young *et al.*, 1979: p. 74) examined were reported to emit detectable light, but neither the gills ($n = 3$) nor the stomach ($n = 1$) did so. Unfortunately, neither the sex nor the feeding status of the bioluminescent bolitaenids was reported.

Materials and Methods

Sixty specimens of *Eledonella pygmaea* (Table I) that share meristic characters of the gill lamellae and suckers are the basis of this study. The sex of each specimen was determined by internal examination: males were identified by the presence of a single genital duct and females by the presence of paired genital ducts; the sex of one individual could not be determined. *G*-tests were used to determine whether the sex composition of the sample differed from unity and whether the presence of senescent females and of juveniles significantly differed with the month of the year. A Wilcoxon two-sample test was used to look for significant size differences between the sexes.

Because accurate measurement required that the specimens be dissected, only 40 of the comparatively rare specimens were measured for this analysis. The 11 measurements recorded included dorsal mantle length, from the midpoint between the eyes to the posterior tip of the mantle; mantle width, measured with the calipers touching the digestive gland through the mantle wall; head width, the maximum width of the head including the eyes; digestive gland length, the maximum length of the organ; posterior salivary gland length, tip to tip on the dorsal surface on the left gland; pupil length, along its longest axis; eye length, along its greatest axis; and arm length, from the first sucker to the arm tip on the oral surface. Arm lengths were averaged within each of the four arm pairs. Additional characters, such as esophageal crop diameter, were not measured because preservation bias caused by the presence or absence of food in the crop at fixation violated assumptions implicit in the application of morphometric analyses to soft-bodied organisms (Voight, 1991) and because clearly defined endpoints on which to base the measurements are absent. In this analysis, preserved specimens of a wide range of sizes are included.

Data were transformed to natural logarithms (ln), a technique that preserves allometries, standardizes variances, and produces a scale-invariant covariance matrix (Jolicoeur, 1963). The ln-transformed data were entered into a principal components analysis (hereafter referred to as PCA) using PROC FACTOR in SAS (SAS Inst., 1987); and principal components (hereafter termed PC)

Table I

Summary of information for the lots of specimens examined: museum catalog number, collection locality, number of specimens, and collection date and depth

Museum number[1]	Latitude (°N)	Longitude (°W)	*N*	Collection month, year	Depth (m)
FMNH 78332**	32°13.3′	64°37′	2	August 1948	730–820
FMNH 278057	32°13′	64°40.5′	1	July 1948	1953
USNM 792006**	32°04′	63°58′	29	August 1971	0–1025
FMNH 78333	32°	64°51.7′	1	July 1948	1000–1100
UMML 31.2564	29°4′	87°37′	1	April 1961	186
UMML 31.171	28°58′	88°00′	1	October 1953	1544–1730
UMML 31.2030*	26°30′	90°42′	1	July 1959	2790
UMML 31.2031*	23°35.25–36.3′	76°54.25–55.1′	1	April 1975	1000
UMML 31.2032	23°59.7–24°1.2′	75°46.75–47.5′	1	November 1974	1900
UMML 31.2033*	23°38.0–40.5′	76°52.4–55.25′	1	August 1975	1000
UMML 31.1701*	23°12.6	90°44.1′	3	November 1975	2000
UMML 31.2207	21°56.3–51′	65°4.0–64°57.5′	1	July 1971	1000
UMML 31.2565	19°16′	65°51′	2	July 1971	7282–7363

[1] FMNH = The Field Museum of Natural History; UMML = The University of Miami Marine Laboratory; USNM = The United States Museum of Natural History.

* Lots with one senescent female; ** lots with two senescent females.

were computed from the covariance matrix (*e.g.* Strauss, 1985). The algorithm requires that individuals without complete data be deleted; due to trawl damage, the number of specimens contributing to the multivariate analysis was limited to 35: 11 males, 23 females, and one unknown.

PCA is a powerful multivariate technique that examines patterns of morphological variation regardless of *a priori* group definitions. Because culturing individuals through the life cycle and analyzing their growth at regular intervals is impossible in this species, this analysis uses each preserved specimen as a proxy for the species at that size. In this manner, analysis of museum specimens quantifies allometric patterns. Analysis of specimens of a wide size range, as in this case, is predicted to reveal that size contributes most morphological variation observed. All measurement data from each specimen entered in the analysis are predicted to reflect, to a greater or lesser extent, the specimen's size, as the parts are expected to increase with increasing size. PCA identifies this unique pattern of strong positive covariance among the characters it analyzes as overall size. This size variation is assigned to a component, usually PC1, that can be recognized by the uniformly large positive loadings of each character. Partitioning size to a single component allows the analysis to consider shape variation without the confounding effects of size. The absolute value of the loading of each character on each component identifies how that character contributes to size (on PC1) and shape variation (on subsequent components). Each specimen is assigned a score on each component; the score signifies its position on that component relative to the others in the analysis.

When PCA revealed that a single measurement—posterior salivary gland length—contributed most size-free shape variation, the natural logarithm of that measurement was plotted against ln mantle length to express the shape variation of the gland in two dimensions. This procedure also increased the number of specimens (12 males and 28 females) contributing to the calculation of the equation of the line describing the growth of the character in members of each sex relative to mantle length.

The distribution of chromatophore organs on the sheath superficial to the crop was compared between males and females, as was the transparency of the sheath. The esophageal crops of nine individuals were opened and their contents examined. To test whether the olfactory papillae (the paired, fan-shaped papillae projecting from the lateral edges of the mantle opening) are sexually dimorphic, as olfactory organs frequently are in fishes from depths of 1000–4000 m (Marshall, 1967), the maximum dimension of the right olfactory papilla was plotted against mantle length for 7 male and 10 female specimens. The papillae detect water-borne chemicals in squids (Gilly and Lucero, 1992); whether the organs function in this manner in octopods is yet to be demonstrated.

Results

As predicted, size contributed most (82.0%) of the morphological variation revealed by PCA (Table II). One measurement, posterior salivary gland length, contributed most of the size-free shape variation (8.48% of the total morphological variation). This variation is due to differences between males and females, as is evident when individual scores on PC2 (size-free shape variation) are plotted against PC1 (overall size variation) (Fig. 2). Digestive gland length contributed most to shape variation on PC3, due largely to data from a single senescent female.

The dimorphism is evident in individuals with mantle lengths greater than 18 mm (Fig. 3). The growth rates of the posterior salivary glands relative to mantle length differed strongly between the sexes. The positively allometric growth of male posterior salivary gland length (PSG) relative to mantle length (ML), with both expressed as natural logs (ln), is described by the equation:

$$\ln \text{PSG} = 2.3\ (\ln \text{ML}) - 4.97.$$

The allometric coefficient of posterior salivary gland length in females is one-fifth of the gland's coefficient in males; its negatively allometric growth is described by the equation:

$$\ln \text{PSG} = 0.46\ (\ln \text{ML}).$$

The dimorphism of posterior salivary gland size appears to correlate with qualitative characters. Although the dis-

Table II

Loadings of each of the 11 characters on the first three principal components (PC) from the analysis of 35 specimens of Eledonella pygmaea

Character	PC1	PC2	PC3
Mantle length	0.941	−0.007	0.178
Mantle width	0.903	−0.135	0.151
Head width	0.950	−0.064	0.106
Digestive gland length	0.787	0.194	0.533
Posterior salivary gland length	0.531	0.834	−0.146
Pupil length	0.716	0.154	0.273
Eye length	0.890	0.015	0.255
Arm length I	0.975	−0.120	−0.092
Arm length II	0.968	−0.120	−0.132
Arm length III	0.984	−0.001	−0.116
Arm length IV	0.966	−0.138	−0.020
Total proportion of variation explained by each component:	82.00	8.48	3.74

PC1 represents overall size variation, as is indicated by the strongly positive loadings for each character. PC2 represents size-free variation in posterior salivary gland length, as is indicated by the character's singularly large loading on PC2. PC3 represents size-free variation in digestive gland length, as is indicated by its high loading.

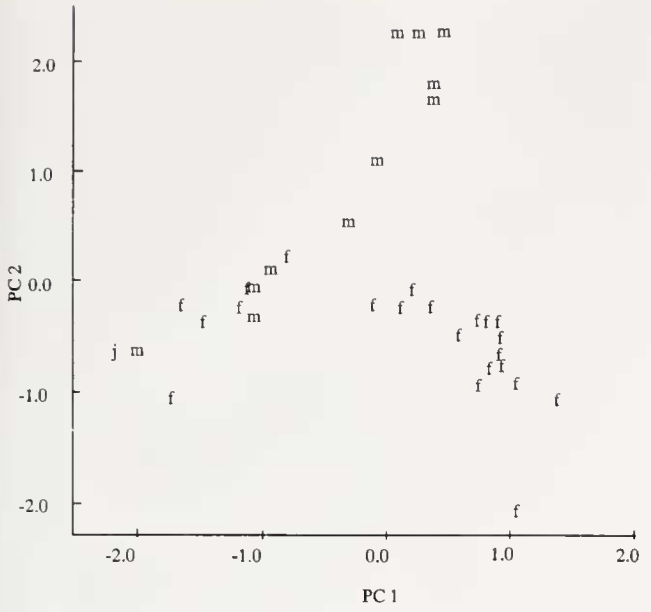

Figure 2. Specimen scores on principal component 2 (PC2) (representing size-free shape variation in posterior salivary gland length) are plotted against scores on principal component 1 (PC1) (representing overall size). m, male specimens; f, female specimens; j, specimen of unknown sex.

tribution of chromatophore organs on the sheath over the dorsal viscera appears to be very nearly the same in both sexes, the transparency of the sheath differs with sex. In preserved males, the silvery iridescence of the sheath effectively obscures the underlying organs; the sheath had to be removed to see the underlying posterior salivary glands that effectively cover the small crop (Fig. 1a). In females, the crop and its contents are readily visible through the sheath; the posterior salivary glands cover only the medial portion of the large crop (Fig. 1b).

The crops of three of the six males examined were empty; the crops of the three other males and all three females contained fish scales, parts of crustacean exoskeletons, and an apparently parasitic worm. The only prey item that was identifiable to species was a conspecific, identified by an arm, in the crop of a female.

The olfactory papillae of males and females were similar in size. Damage to the skin overlying the eye appeared to be associated with distortion of the papillae, regardless of the sex of the specimen.

The sex ratio was significantly female-biased (38 females to 21 males, $G = 4.97$; $p < 0.05$). Among the specimens examined, the incidence of individuals smaller than 10 mm mantle length did not significantly differ among the months for which samples were available ($G = 1.39$; $p > 0.05$). Of the specimens analyzed, those with the longest mantles, the traditional estimator of cephalopod size (Fig. 3), and with the highest PC1 scores (Fig. 2) were female. The PC1 scores of males and females did not, however, significantly differ (Wilcoxon two-sample test, $t = 1.49$; $p > 0.40$).

Eight of the 38 females examined appeared to be reproductively mature or nearing senescence. The largest ovarian eggs found in a female were 1.85 mm long, only 0.15 mm less than the longest egg definitively reported as being from a specimen of *Eledonella* (Young, 1978); no hatchlings were present. The incidence of senescent females did not significantly differ among the months for which samples were available ($G = 1.16$; $p > 0.05$). The collection depths of the post-brooding, senescent females are uninformative about the depth at which mating occurs. Among the male specimens examined, none were reproductively mature, *i.e.*, none contained spermatophores; but males with enlarged reproductive organs were found, and these were probably nearing sexual maturity.

Discussion

The growth rate, relative to the mantle length, of the posterior salivary glands is five times faster in males of *Eledonella pygmaea* than it is in females, and as a result, the glands of males are up to two-and-a-half times larger than those of conspecific females of similar size (Fig. 1). Relying on distributional data from Young (1978) and our limited biological knowledge of the species, I argue

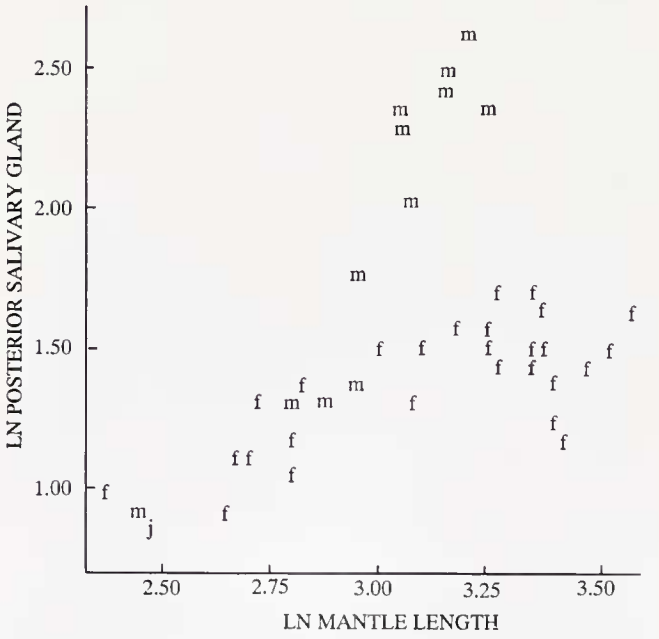

Figure 3. The natural logarithm (ln) of posterior salivary gland length is plotted against ln mantle length for 40 individuals of *Eledonella pygmaea* m, male specimens; f, female specimens; j, specimen of unknown sex. For the equations of the lines describing the glands growth in males and females, see text.

that this sexual dimorphism results from the adaptation of males to their deep-water habitat. Further, I posit that inferred sex-specific selective forces are responsible for sexually dimorphic depth distributions.

To discuss the evolution of a character, its primitive condition must be established, and in this case, I consider small posterior salivary glands to be the ancestral condition. The Bolitaenidae appears to be the basal lineage of the suborder Incirrata (Voight, unpub. data). Members of the sister taxon, the suborder Cirrata, lack posterior salivary glands in the mantle cavity; the glands of the outgroup, the order Vampyromorpha, are very small (Young, 1964). Sexual dimorphism of the glands and the particularly large size they reach in males appear to be uniquely shared among bolitaenid species (Voight, unpub. data).

Given the difficulties in observing bolitaenids in nature, we must infer how selective pressures on males and females differ, as differences are required for sexual dimorphism to evolve. Selection acts to increase the depth distribution of males. A corollary to Young's (1978) hypothesis that bolitaenids mate at great depths predicts that mature males occur at those depths to increase the number of receptive females they encounter. Selection also acts to intensify the sensitivity of males to light cues and to increase male mobility. Because responding to a female's light cue increases a male's chances of mating (Robison and Young, 1981), males that are better able to detect bioluminescence will have higher fitness. To further increase the number of receptive females that they detect, males should be highly mobile. Males that move across broad areas are likely to see more mates than are males who search only locally. The absence of mature males from trawl collections (this study, $n = 60$; Young, 1978, $n = 80$), if due to net avoidance, supports the hypothesis of increased male mobility.

In females, selection acts to increase fecundity, a feature tightly linked to body size in cephalopods (Mangold, 1987). To grow large rapidly, females may remain in comparatively shallow depths where the crustaceans and fishes that females and juvenile males exploit as prey are more abundant. Females descend to greater depths only when ready to mate. Selection will not heighten sensitivity to bioluminescence or increase mobility in females, except to the extent that the traits are under selection in conspecific males.

The sex-specific selective forces outlined above suggest that the variability in size at which bolitaenids descend to adult depths documented by Young (1978) is sex-linked. Reproductively mature males occur at the lower end of the species' depth range; females occur at these depths only when ready to mate. If this hypothesis of habitat-partitioning between the sexes is supported, the evolution of large posterior salivary glands in males can be argued to relate to ecological factors.

As mature males descend in the water column, the abundance of familiar prey declines, and their energy costs may increase. Males must pay the metabolic costs thought to be associated with high visual acuity (Childress, 1995) if they are to detect mates. To meet these metabolic demands, maintain their capacity for high mobility, and prolong their survival in this habitat, I suggest that males use their visual acuity to exploit bioluminescent prey, which increases in abundance with depth.

The shift, with depth, to the selection of bioluminescent prey carries with it a major liability. A translucent bolitaenid risks predation if prey in its crop emits light. Enlarged posterior salivary glands, however, reduce the risk of predation in two ways. First, the large glands, and the iridescence of the sheath overlying the dorsal viscera, effectively cover the crop of males and would physically block light emitted from within it. Second, assuming that large glands release greater volumes of proteolytic enzymes than do small glands, large glands would speed the catabolism of bioluminescent chemicals.

One could argue that, if gland size correlates with the potency or volume of the proteolytic enzymes released, males with large glands would digest prey more quickly, lowering their energetic cost of swimming, but the digestive gland is a primary site of food absorption in cephalopods (Boucaud-Camou and Boucher-Rodoni, 1983). Therefore, if males were under selection to maintain constant body weight by speeding the digestion and absorption of prey, the digestive gland should also be dimorphic. PCA falsifies this prediction (Table II).

Alternatively, one could argue that females face a similar liability. Among octopuses, however, gravid females are rarely active predators. As their eggs enlarge, females typically reduce their feeding rates (Mangold, 1987). If this generalization holds true for bolitaenids, gravid females are not likely to ingest prey while near the lower limits of the species range. This physiological pattern also argues against sexual cannibalism as a routine strategy in the species. Although sexual cannibalism explains the presence of a conspecific in the crop of a female, so does the animal having fed in the trawl. Sexual cannibalism also explains the rarity of mature males, as does the hypothesis of increased male mobility.

The presence of sexually dimorphic posterior salivary glands was unsuspected in this taxon. This striking difference in the digestive system had been attributed to dissimilar nutritional states of the specimens (Thore, 1949) and to the existence of cryptic species (Young, 1972b). Indeed, sex-linked differences have not been noted in any of the taxonomically diverse deep-sea predators in which dark peritoneums or digestive organs have been suggested to camouflage bioluminescent prey (*e.g.*, vampyromorph

cephalopods, Pickford, 1949; fishes, McAllister, 1961). The rarity with which deep-sea animals such as these are seen in nature may limit our ability to document a sex-linked difference, especially if the sexes partition habitats, as suggested here.

If the posterior salivary glands camouflage ingested luminescent prey as effectively as this study indicates, direct observation of living animals may not detect their presence. Museum specimens collected incidentally in the previous half century through a variety of research efforts do, however, provide the anatomical and allometric data that are critical not only to documenting the patterns, but to generating this hypothesis of its evolution, including polarity assessment. Although the hypotheses could not have been generated using observations of live animals, the critical tests of the hypotheses—determining prey preferences and energetic costs experienced by males at depth—cannot be conducted on preserved specimens. Expanding the techniques we apply to the study of these rare deep-sea animals will increase our knowledge of one of the least-known habitats of the world, the mid-water depths, and provide evolutionary insight into questions of broad importance and biological complexity.

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